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Diurnal and Seasonal Behavior Patterns Among Adults of *Protoxaea gloriosa* (Hymenoptera, Oxaeidae)

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ABSTRACT

Each season, males of *Protoxaea gloriosa* (Fox) emerge from the ground and establish territories near nectar plants several days before the females appear. The first seasonal emergence of females occurs near midmorning and they immediately seek nectar. During this initial flight mating normally takes place, usually on the nectar flowers. Within 10 days to two weeks most of the females have constructed burrows, are collecting pollen, and are provisioning cells. Activity begins at approximately sunrise when working such plants as *Solanum* and *Cassia* and continues for two or three hours before collecting ceases and the burrows are closed (they are opened briefly near midday for an additional nectar flight). When working flowers of *Kallstroemia*, which do not open until well after sunrise and produce an overabundance of pollen, collecting by some individuals may extend to noon or later.

As the season progresses male territories shift with changes in female pollen-collecting patterns but this activity usually peaks near midmorning after most collecting has ceased. By early afternoon, the previously antagonistic males begin to cluster in large aggregations on selected plants where they spend the night. Temperatures in the clusters fluctuate but, during observations through the night, mostly ranged from 20.5°C. to 25.5°C. with air temperatures ranging downward from 23.5°C. to 18°C. When disturbed, the cluster temperatures rose suddenly by 8 to 10°C.

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INTRODUCTION

The genera *Protoxaea* Cockerell and Porter (1899) and *Oxaea* Klug (1807) are two apparently related Western Hemisphere genera. The former genus contains a number of nominal species and subspecies in southwestern United States and Mexico (Linsley, 1951; Linsley and Michener, 1962) and at least one species in Brazil, Paraguay, and Argentina (Moure, 1944, 1947). *Oxaea* comprises species that, with one exception, are limited to the Guiana-Brazilian geographical subregion (Moure and Seabra, 1962). *Oxaea fuscescens* Sichel extends from Caracas, Venezuela, to S. Geronimo, Guatemala (Moure and Urban, 1963). Together, *Protoxaea* and *Oxaea* represent an anomalous group of large, hairy, fast-flying bees, the phylogenetic affinities of which are uncertain. For example, Klug (1807) who named the genus *Oxaea* was unable to relate it to any other known genus of bees. Latreille (1810) placed it among the parasitic bees near *Melecta* and *Crocisa* and F. Smith (1854) assigned it between *Xenoglossa* and *Melitturga* near *Xylocopa* and *Lestis*. Sichel (1865) expressed the view that the true position of the genus was near the end of the tribe Xylocopites of Lepeletier (1841). Gerstaecker (1867) suggested an andrenine relationship, and Dalla Torre (1896) placed it in the Anthophoritae between *Diphaglossa* and *Lestis*. Friese (1898), who gave *Oxaea* (including species later assigned to *Protoxaea*) the most extensive study up to that date, considered them to be derivatives of the colletid group now designated as the caupolicanine branch of the Diphaglossinae, and derived the Old World genus *Melitturga* from this primarily Neotropical group. A year later, Ashmead (1899) transferred *Oxaea* from the Colletidae to the Xylocopidae (*sensu stricto*) and in 1902 Schrottky placed it next to *Megacilissa* in the Andrenidae, separating both genera from *Caupolicana* and *Diphaglossa*. Bischoff (1934), calling attention to some previously unused characters in bee classification, listed some features shared by *Oxaea* and genera currently placed in the Andrenidae as well as some that are not, but although he tabulated generic characters he did not provide a classification which indicated his views as to relationships among the bee genera which he studied. On the other hand, Popov (1941, 1945), who proposed family status for the Oxacidae, regarded certain of the characters shared with andrenids and *Nomada*-like parasitic anthophorids as convergence. Michener (1944) in his classical work on the phylogeny and classification of the bees, relying heavily on the presence of subantennal sutures, assigned *Oxaea* and *Protoxaea* to the Andrenidae, proposing for their reception the subfamily Oxacinae, noting apparent affinities with the andrenine

genus *Melitturga* (subfamily Panurginae). However, he stated that "it appears to me a matter of choice whether one wishes to regard the Oxaeinae as a distinct family or not. The Oxaeinae are more distinct than the subfamilies within other families of bees, including the Apidae in the sense in which I use it." Moure and Seabra (1962) apparently accepted the conclusion that the group was andrenine.

Data available to Friese, Michener, Moure, and their predecessors that had a bearing on the phylogenetic relationships of *Oxaea* and *Protoxaea* were limited to comparative adult morphology. Rozen (1964), after studying first and last instar larvae of *Protoxaea gloriosa* found anomalies in the structures of these, particularly the third instar which shared characters with some of the *Nomada*-like parasitic anthophorids. However, he also regarded these similarities as expressions of convergent evolution. Because most of the characters that larval *Protoxaea* share with known larval andrenids are also found among the Colletidae, Halictidae, and to some extent the Melittidae, he considered them of little value in determining relationships. Rejecting affinities with *Melitturga* because of fundamental differences in the male genitalia, Rozen suggested elevating the oxaeines to family status and proposed that if this were done, their relationships with the colletid Stenotritinae might well be reviewed at the same time. Later, Rozen (1965), basing himself on further studies of *Melitturga* and the morphological characters common to other andrenids, reaccorded the group family rank without, however, assigning it a specific phylogenetic position, although he concluded that it probably diverged early from the evolutionary lines that gave rise to the higher bees. Stephen, Bohart, and Torchio (1969, pp. 44-45), in their conspectus of bee families placed the Oxaeidae between the Halictidae and Anthophoridae; in their systematic presentation (1969, p. 50), between the Andrenidae and Melittidae.

Another source of data, which taken with that already available from others, is behavioral. Our observations on nest structure, cell formation, and larval development of *Protoxaea gloriosa*, *Ptiloglossa jonesi* Timberlake, and *Caupolicana yarrowi* (Cresson) have not yet been fully analyzed, but we hope to present them in comparative terms in the near future. In the meantime, we offer additional data on adult behavior of *Protoxaea gloriosa*, some of which may prove to have phylogenetic significance. Linsley and Michener (1962) have already published considerable information on adult activity and this has been supplemented by Cazier and Linsley (1963) with regard to male territoriality and Linsley and Cazier (1963) with respect to pollen competition. It is the object of the present paper to

integrate these earlier observations with new data since obtained and to provide some comparisons with adult behavior of caupolicanine bees which inhabit much the same area (Linsley and Cazier, 1970).

LOCALITIES INVOLVED IN THE STUDY

Protoxaea gloriosa was described by Fox (1893) from specimens collected in Las Cruces, New Mexico. It has subsequently been found from Texas to Arizona along the Mexican border and in adjacent areas of northern Mexico. Its total range remains unknown.

The localities in which we have conducted field studies of adult behavior, both those reported previously and those discussed here for the first time, are mostly situated in southeastern Arizona (Cochise County) and southwestern New Mexico (Hidalgo County). The more important of these from the viewpoint of the present paper are, from south to north: (1) an area one mile east of Douglas, Arizona, close to the Mexican border; (2) sites within a few miles of Portal, Arizona, and (3) others near Rodeo; New Mexico.

The Douglas site (described by Cazier and Linsley, 1963) was about 450 meters long, north and south, by about 90 meters wide, east and west, extending along a drainage dike which had been scraped up from both sides. All the observations were made on the gently sloping east side of the dike where many kinds of annual and perennial herbs were in bloom, sparsely intermixed with several species of shrubs. The area was surrounded by a rather dense stand of *Larrea tridentata* (De Candolle) Coville with a scattering of *Prosopis juliflora* (Swartz) De Candolle. Some of the *Larrea* bushes still had flowers but the *Prosopis* was devoid of blossoms.

When this site was first studied (Cazier and Linsley, 1963), the most conspicuous flowering herbaceous plants, arranged roughly in the order of their abundance, were: *Lepidium montanum* var. *canescens* (Thellung) C. L. Hitchcock, peppergrass; *Verbesina encelioides* var. *exauriculata* Richard and Galeotti, crown-beard; *Solanum elaeagnifolium* Cavanilles, horse nettle; *Baileya multiradiata* Harvey and Gray, desert marigold; *Mentzelia pumila* (Nuttall) Torrey and Gray, stickleaf; *Xanthium saccharatum* Wallroth, cocklebur; *Hoffmanseggia densiflora* Benthams, hog potato; *Solanum rostratum* Dunal, buffalo bur; *Conyza coulteri* Gray; *Cucurbita foetidissima* Humboldt, Bonpland and Kunth, buffalo gourd; *Cucurbita digitata* Gray, finger leaf gourd; *Asclepias subverticillata* (Gray) Vail, poison or horsetail milkweed; *Datura quercifolia* Humboldt, Bonpland, and Kunth, thorn apple; *Argemone platyceras* Link and Otto, prickly poppy; and numerous less abundant or conspicuous annuals. In addition to *Larrea* and *Prosopis* there were scattered shrubs of *Parthenium incanum* Humboldt, Bonpland, and Kunth,

mariola; *Lycium* sp., wolfberry or desert thorn; bird-of-paradise flower, and tar-or-varnish-bush. In the intervening years this site has been increasingly disturbed and we have not again encountered this amount of floral diversity.

Portal, Arizona (elevation 4700 feet) is situated in a riparian area with intermittent streams at the mouth of Cave Creek Canyon. The principal sites involved in *Protoxaea* studies were 2.5 miles north in rangeland dominated by thorn scrub where a man-made catch basin ("tank"), designed to hold water for cattle, had largely been taken over by the shrub composite *Baccharis glutinosa* Persoon, which is known locally by a variety of names, including "seep willow," and is a highly attractive nectar plant, drawing large numbers of aculeate Hymenoptera and their predators from the surrounding arid environment. Other areas near Portal were mostly in open, dry rangeland in the thorn scrub east of Portal where flowering of many perennial plants is dependent on winter or spring precipitation, and the remaining perennials and practically all annuals on summer rainfall. These facts cause tremendous fluctuations in the composition of the flora from season to season and thus of the pollinators. *Protoxaea gloriosa* and its larger caupolicanine competitors appear to be able to adjust to these variations by means of their capacities for rapid, long distance flight.

The most important of these sites near Portal was that utilized for 1970 pollen competition studies. It was situated 2 miles northeast of Portal (2.5 miles by road) on an alluvial fan sloping gently upward to the southwest of the San Simon Road for 100 yards. The soil consisted of decomposed Paradise limestone with numerous surface rocks and leached caliche from the underlying formation. At the upper end, this site was 90 yards wide, along the roadway 40 yards. Of this area it was estimated that almost an acre represented open sites with a low cover dominated by the legume *Cassia bauhinioides* Gray which averaged from five to 11 plants per square yard between scattered shrubs of creosote bush (*Larrea tridentata*), mesquite (*Prosopis juliflora*), catclaw (*Acacia greggii* Gray), whitethorn, (*Acacia constricta* Benthams), tar-bush (*Flourensia cernua* De Candolle), salt bush (*Atriplex canescens* (Pursh) Nuttall), and a few examples of *Yucca elata* Engelmann, ocotillo (*Fouquieria splendens* Engelmann), cactus (*Opuntia* sp. and *Cylindropuntia*). Growing among the *Cassia* plants was the grass *Tridens pulchellus* (Humboldt, Bonpland, and Kunth) Hitchcock and various other low-growing plants including annual and perennial herbs and vines. These included the white-flowered *Zinnia pumila* Gray, which was very conspicuous in the early morning hours, *Sphaeralcea laxa* Wootton and Standley, *Parthenium incanum*, *Allionia incarnata* Linnaeus, *Baileya multiradiata*, *Croton*

sp., *Gutierrezia microcephala* (De Candolle) Gray, *Pectis papposa* Harvey and Gray, *Eriogonum fasciculatum* Benthams, *Apodanthera undulata* Gray, and a few additional species in very small numbers.

Another important site near Portal was 2 miles east of this locality. The site involved an open meadow surrounded primarily by *Acacia* and *Prosopis* to the north and east and by *Larrea* on the south and west. The area was about 100 by 200 yards densely covered with *Kallstroemia grandiflora* Torrey in the summers of 1970 and 1971. There were a few perennial shrubs in bloom including scattered plants of *Acacia constricta*, *Larrea tridentata*, *Prosopis juliflora*, *Mimosa biuncifera* Benthams, *Ephedra trifurca* Torrey, *Flourensia cernua* and *Parthenium incanum*.

Also in abundance and mixed in with the *Kallstroemia* were blooming *Baileya multiradiata*, *Gutierrezia microcephala*, *Eriogonum abertianum* Torrey, *Allionia incarnata*, *Zinnia pumila*, *Eriogonum fasciculatum*, *Lepidium montanum* Nuttall and *Pectis papposa*.

The principal Rodeo study site is on the gentle slope and low bench (30 to 40 feet high) along the east side of the old San Simon River drainage. The river bottom area immediately west of the area is no longer connected with the San Simon River so that water accumulates in the lower portions and disappears by percolation or evaporation. The soil consists primarily of a heavy clay loam in the bottom with scattered sandy areas around the edges. The primary vegetative cover is the perennial shrub *Ephedra trifurca* and the perennial grass *Hilaria mutica* (Buckley) Benthams. Mixed with these are a number of other species of grasses and after the rains numerous annual herbs.

The eastern slope and low bench, the top of which flattens out toward the base of the Peloncillo Mountains, is an area of sandy soil with scattered small surface gravel. Along the western exposure of the slope there are several areas where the caliche has been exposed by erosion, otherwise this hard calcareous material underlies the sandy soil at depths of from 35 to 50 cm. The principal nesting area for *Protoxaea* and some of its pollen competitors was situated in a shallow impression measuring about 20 meters in width, north by south, and 50 meters in length, east by west, extending from the flattened area on top down the west-facing slope. The south-facing slope of the impression was at a slightly steeper angle than the north-facing portion, parts of which graded almost level into the surrounding area. The south-facing slope had more surface gravel exposed and also had more *Protoxaea* nests than the remainder of the area. The vegetative cover of this slope bench was more diversified than that in the adjacent bottom land to the west or on the level terrain extending eastward.

The nesting area was generally open with widely scattered plants of the perennial shrubs *Ephedra trifurca*, *Lycium* sp., *Yucca elata* and the perennial herbs *Apodanthera undulata*, *Euphorbia albomarginata* Torrey and Gray, *Euphorbia* sp., and *Gutierrezia microcephala*. With the exception of a few small spots, the entire area was covered with closely spaced plants of the perennial grass *Tridens pulchellus*. Sparsely intermixed and sometimes in localized spots within the area were plants of the annual herbs, *Gilia longiflora* (Torrey) G. Don, *Eriogonum* sp. (purple flowered), *Eriogonum trichopes* Torrey, *Cassia bauhinioides*, *Salsola kali* Linnaeus, *Tidestromia lanuginosa* (Nuttall) Standley, *Solanum elaeagnifolium*, and *Gaillardia pulchella* Fougereux. Around the immediate periphery, and in addition to the above, there were patches of isolated plants of the annual herbs *Baileya multiradiata*, *Bahia absinthifolia* var. *dealbata* Gray, *Eriogonum abertianum*, and *Lepidium montanum* var. *canescens*. Within about 1/4 mile toward the north and east there were a few (six or eight) plants of the annual herb *Kallstroemia grandiflora* and beginning on the north and west edge of the area and extending north for about 1/4 mile were scattered thickets and isolated bushes of the perennial shrub *Koeberlinia spinosa* Zuccagni and scattered plants of the perennial herb *Hoffmanseggia jamesii* Torrey and Gray.

A second site near Rodeo, along the shoulders of the Portal Road on the New Mexico side of the Arizona-New Mexico state line, provided opportunities for studies of competition among flower visitors to *Kallstroemia grandiflora*, *Solanum elaeagnifolium*, *Cassia bauhinioides*, and *Calliandra schottii* Torrey, and the relative attractiveness of these plants to *Protoxaea gloriosa* when growing together.

EMERGENCE OF MALES AND ESTABLISHMENT OF TERRITORIES

Male *Protoxaea* at the study sites at Douglas, vicinity of Portal, and near Rodeo, were first seen taking nectar and establishing territories several days before females were in evidence. On July 29, 1963, near Rodeo, they were establishing territories near thickets or individual shrubs of *Koeberlinia spinosa*, which were being visited for nectar by large numbers of aculeate Hymenoptera, including occasional newly emerged female *Protoxaea* receptive to mating. During the next 10 days, 33 males in territory were captured and marked with colored disks of a type that we had used successfully with female bees. Of the marked bees, only three returned to their old territories. Territories of all but nine of the remainder were taken over by unmarked males. On the first day 11 of the marked males were replaced, six immediately or within 15 minutes, three between 23 and 64

minutes, and two approximately 90 minutes later. Five more of the vacated territories were re-occupied on each of the next two days and two on the fourth day.

On August 8, female *Protoxaea* began gathering pollen in the early morning from *Cassia bauhinioides*. By August 10, all males had left *Koeberlinia* and shifted their territories, mostly adjacent to or above patches of *Cassia* (however, a few individuals selected plants of *Ephedra*, *Lycium*, or *Gutierrezia*). Although the females worked the *Cassia* flowers primarily at about sunrise, males rarely appeared in their territories before mid-morning when the flowers were closed.

Also, on August 8, the first females were observed taking pollen from *Lepidium montanum* var. *canescens* and males began to establish territories near these plants. Some males established unstable territories near the principal nearby area of female nesting activity, but as the season progressed and greater use was made of pollens from *Solanum elaeagnifolium* and *Kallstroemia grandiflora*, the males did not establish territories near these plants (at other sites where *Kallstroemia* was the dominant flowering plant and females were actively gathering pollen, males established territories over groups of the plants or adjacent to shrubs overlooking the plants). Furthermore, pollen-gathering females that did enter the territories of guarding males were ignored, although other male *Protoxaea* and large flying insects of all kinds were attacked.

These observations reinforce the tentative conclusions of Cazier and Linsley (1963) that the principal function of male territoriality in *Protoxaea* is to assure the immediate mating of newly emerged females through spacing and coverage of appropriate nectar plants. Because nesting females are apparently ignored by males, territorial belligerence toward other insects in the vicinity of pollen sources may reduce competitive pressure on the females. However, at the principal Rodeo site, territorial activity of males and pollen-gathering activity of females were out of phase, the latter usually having completed their morning foraging before the males arrived in their territories.

Rozen (1965), in commenting on similarities in structure and behavior between the males of oxaeids and *Melitturga*, including the structure of the eyes, thorax, and hovering and darting behavior of individuals in territories, regarded them as analogous rather than homologous, and seemingly "referable to a single functional trait, namely, the premating and perhaps mating behavior of the males." This suggestion, which emphasizes premating (and presumably territorial) behavior, has been expanded into a much stronger statement by Stephen, Bohart, and Torchio (1969), that "there is an interesting convergence between males of *Apis*, *Oxaeidae*,

Melitturga (a Palearctic panurgine), and *Caupolicana* (Neotropical colletid). They all have enlarged compound eyes, ocelli low on the face, elongate first flagellar segments, boxlike thorax,¹ short abdomen, and long, thin legs that hang downwards in flight. The similar mating habit, in which males hover beneath the females and dart upwards after them in flight, apparently has been responsible for this convergence." The portions of this conclusion that relate to mating behavior do not apply to *Protoxaea gloriosa*, which, as has been pointed out by Linsley and Michener (1962) and confirmed by us in many subsequent observations, mates on flowers. Further, the males do not suspend the legs except when poised in territory; they retract them immediately when involved in forward flight (see Cazier and Linsley, 1963), a situation in which hanging legs would place a "drag" on flight progress.

FEMALE EMERGENCE, MATING, AND FORAGING

We have already emphasized that females begin to emerge some days later in the season than the males. At Douglas on July 26, 1962, the day after the first soaking rain on the study area, 103 males and seven females were seen in contrast to six males observed the previous 10 days. Thus, apparently moisture triggers emergence, at least in the arid Southwest.

The freshly emerged female usually leaves on her first flight between 8:30 and 10 AM, immediately seeking nectar. At this time she is receptive to mating and, by selecting the nearest nectar source to the emergence site, she is almost invariably contacted immediately by a watchful male and impregnated. Linsley and Michener (1962) have described the mating process, during which the male forces his head between the propodeum of the female and the first metasomal segment, the base of which is grasped by the mandibles. This procedure is critical because in the numerous matings observed by us, one or more additional males have attempted to dislodge the primary individual. Even if a mating pair is disturbed and the female flies off with sexual contact broken, the male retains his grip with the mandibles and clings during flight. As reported by Linsley and Michener, the later males appear to be unable to dislodge the first, and in the observed cases, the primary male was usually the larger of the two.

Protoxaea gloriosa is a polylectic bee which takes pollen from a taxonomically diverse group of plants, including *Lepidium montanum* var. *canescens* (Cruciferae), *Cassia bauhinoides* (Leguminosae), *Kallstroemia grandiflora*

¹ This description does not agree with our interpretation of the shape of the thorax in these bees.

(Zygophyllaceae), and *Solanum elaeagnifolium* and *S. rostratum* (Solanaceae). The pollen produced by these species varies in size from an average diameter of 25.6 for *Solanum* to 66.7 microns for *Kallstroemia* (Linsley and Michener, 1962). However, *Cassia*, as reported by various writers, produces two sizes of pollen. The large grains, averaging approximately 20 percent in our samples were about 80 microns in diameter. The majority, which unlike the aborted pollen of *Solanum*, included stainable protoplasm, were approximately 27 microns in diameter. Peter Raven examined 2565 pollen grains—a minor sample from each of three *Protoxaea* of which 2015 (79 percent) were of the small-grained type. These latter have been interpreted as a “bonus” to bee visitors.

The form of the flower in these host plants also differs markedly: small, regular, and racemose (*Lepidium*); large, open, poppy-like, with orbicular anthers (*Kallstroemia*); heads with long conspicuous stamens (*Calliandra*); moderate-sized, regular, rotate, with tubular anthers (*Cassia*). The flowers appear to the human eye white, yellow, bluish, and yellow-orange.

Linsley and Cazier (1963) have described the nature of the specialized pollen-holding devices (scopae) in *Protoxaea*, which appear to be well adapted for transport of small pollen grains. They consist of specialized scopal hairs on the posterior coxae, trochanters, femora, the anterior surface of posterior tibiae, and dorsal one-fourth of anterior surface of posterior basitarsi, and sides of the propodeum and first metasomal tergum, as well as the middle of the first metasomal sternum. Scopal hairs are long, pale yellow-brown, dense, somewhat curved, with whorled branches. Hairs of the coxae are curled apically and become shorter toward the base; those of the trochanter are curled apically; those of the femora, ventrally and apically. Hairs of dorsal surface of tibiae and dorsal one-fourth of anterior surface of hind basitarsi, shorter, straight, and directed apically, those of ventral surface, longer, curled ventrally and somewhat apically. On the inner faces of the posterior tibiae, hairs are shorter, moderately dense, simple, stiff, and directed ventrally. On the lateral face of the propodeum they are directed posteriorly and ventrally, on sides of the first metasomal segment, ventrally, and on the middle of the first metasomal sternum, posteriorly. The pollen is packed dry. When extracting pollen from *Cassia* and *Solanum*, the bee must vibrate the tubular anthers and shake the grains from the terminal opening; in the case of *Kallstroemia* the pollen-collecting female literally wallows in the anthers grasping them with the legs as she simultaneously rotates with her mouthparts probing the nectaries. In the process most of the body becomes covered with the bright reddish pollen.

Linsley and Cazier (1963) have presented data on foraging and com-

petitive relationships for a number of bee species, including *Protoxaea gloriosa*, which were taking pollen from *Solanum rostratum* and *S. elaeagnifolium* at the Douglas site. These, and an undetermined plant with pollen suggestive of *Mentzelia* are the principal pollen sources for *Protoxaea* at this location. On a clear day in mid-August the first female *Protoxaea* appeared at the flowers of *Solanum rostratum* about 15 minutes before sunrise. This was an unusually early arrival, as our observations here and elsewhere indicate that the first females usually arrive just as the sun is rising or shortly thereafter. Nevertheless, this was about a half hour after her principal early competitors, the large caupolicanine colletids *Ptiloglossa jonesi* and *Caupolicana yarrowi*, began working the flowers for pollen, and about 15 minutes after the large bumblebee *Bombus sonorus* Say started pollen collecting. However, the main foraging period for *Protoxaea* extended over a period of three and one-half hours beginning at sunrise as colletid activity was falling off. During this time, its primary pollen competitors were *Bombus sonorus*, which outnumbered *Protoxaea* about three to one, and *Centris atripes* Mocsáry, which were about half as numerous as *Protoxaea*. Similar relationships were evident at flowers of *Solanum elaeagnifolium*, although pollen competitors other than *Bombus* were few during the principal foraging period.

On the following day, under a broken cloudy sky, again two female *Protoxaea* arrived at *Solanum* 15 minutes before sunrise, about an hour and 20 minutes before the main flight began. Under the overcast, this main flight began about an hour later than usual at both species of *Solanum* and extended only over a two-hour period, ending about 9 AM, somewhat earlier than previously. However, *Ptiloglossa* and *Caupolicana* extended their foraging periods during the cloudy period, with *C. yarrowi* providing *Protoxaea* with some pollen competition throughout the pollen collecting period. Also, pollen competition from other bees was more intense during the latter part of the period, notably that provided by three species of *Centris*, *C. caesalpiniae* Cockerell, *C. rhodopus* Cockerell, and *C. atripes*. However, regardless of weather effects, the most consistent and critical pollen competitors at the Douglas site were *Ptiloglossa jonesi* and *Caupolicana yarrowi*, which invariably preceded *Protoxaea* at the flowers, and because of their large size, fast flight, and rapid manipulation of the anthers had already made significant inroads on the pollen supply. *Bombus sonorus*, which invariably outnumbered the *Protoxaea*, provided competition throughout the activity period. The species composition of the other competitors during the latter part of the period varied from day to day as did the number of individuals represented.

During the 1970 season, there was an opportunity to study competitive

TABLE 1
COMBINED MATINAL COLLECTION OF *Protopaxaea gloriosa* AND POLLEN-GATHERING COMPETITORS AT *Cassia bauhinoides*^a

	Before Sunrise					After Sunrise						
	80 min.	60 min.	40 min.	20 min.	0 (sun)	20 min.	40 min.	60 min.	80 min.	100 min.	120 min.	140 min.
<i>Philoglossa arizonensis</i>	0	8	34	57	54	40	26	14	5	0	0	0
<i>Caulopoliana yarrowi</i>	0	3	10	10	6	5	0	0	0	0	0	0
<i>Protopaxaea gloriosa</i>	0	0	1	4	24	58	27	29	21	12	2	0

^a Two miles north of Portal, Arizona, August 15, 19, and 21, 1970.

Time intervals are 20 minutes each. The 80 minutes at left represents 80 minutes to 1 hour before sunrise; the 140 minutes at right, 2 hours and 20 minutes to 2 hours and 40 minutes after sunrise. The samples were taken on clear, bright days after moonlit nights with air temperatures during the first time interval before sunrise varying from 17°C. to 18°C. and during the last time interval after sunrise from 24°C. to 27°C.

relationships of *Protopaea* to two large, aggressive caupolicanine bees, *Ptiloglossa arizonensis* Timberlake and *Caupolicana yarrowi*, in an extensive field of *Cassia bauhinioides* at the locality 2 miles north of Portal, Arizona. On clear bright days, *Ptiloglossa* were actively gathering pollen from an hour before, until an hour after, sunrise, reaching a peak of activity just before the rays of the sun touched the flowers (table 1). *Caupolicana* were far less numerous, peaked at about the same time, but fell off rapidly after sunrise. *Protopaea*, on the other hand, were scarcely evident before sunrise, were most abundant during the next hour, and completed pollen collecting an hour later. On overcast days or mornings following a night of rain, pollen-collecting activity was delayed (table 2). Although both *Ptiloglossa* and *Caupolicana* exhibited aggressive behavior toward *Protopaea* females, occasionally knocking them off of the flowers, the pollen supply was more than adequate to meet the needs of all three species.

At the Rodeo site, it was possible to correlate nest site activities with foraging at a nearby patch of *Cassia bauhinioides* in mid-August. During a three-day period in which the sunrise on the first day was at approximately 6:05 AM, the active burrows were already open when the site was visited at 5:30 AM and the *Cassia* flowers were open and being visited by *Caupolicana yarrowi*. On August 15, a female left her burrow for the first time as the sun was rising, flew to the *Cassia* patch, and returned with a load of pollen nine minutes later. After two minutes in the burrow she made another pollen trip lasting 12 minutes, followed by a third of 18 minutes, and a fourth of 10 minutes. At 7:03 AM, three minutes after her return from the last pollen trip, she made a 10-minute trip for nectar, closing her burrow two minutes later. Air temperatures during the flight periods ranged from 20.5°C. to 22.5°C. At 12 M she reopened her burrow again and left for a 36-minute nectar trip. The air temperature at this time was 33°C. The next morning she made two pollen trips between 6:04 AM (two minutes before sunrise) and 7:02 AM, one lasting 31 minutes, the other 25, followed by two nectar flights of 10 minutes and six minutes duration, respectively. Air temperatures during these four flights ranged from 20°C. to 22.3°C. When the burrow entrance was closed, 16 minutes after the last nectar flight the air temperature had reached 24°C. The midday nectar flight characteristic of this species took place at 11:40 AM and lasted only eight minutes.

This kind of activity pattern was characteristic of all the females with established nests. However, on the first pollen flight of a newly nesting female, the flight periods may be longer. Such females fly more slowly and work over all or almost all the open flowers on one plant before moving to another, spending three or four seconds at each flower. Experienced

TABLE 2
MATINAL COLLECTION OF *Protaxaea gloriosa* AND POLLEN COMPETITORS AT *Cassia bauhnioides*^a

	Before Sunrise					After Sunrise						
	80 min.	60 min.	40 min.	20 min.	0 (sun)	20 min.	40 min.	60 min.	80 min.	100 min.	120 min.	140 min.
<i>Ptiloglossa arizonensis</i>	0	0	6	17	13	14	8	3	2	0	0	0
<i>Cauloplicana yarrowi</i>	0	0	0	0	0	0	0	3	3	2	0	0
<i>Protaxaea gloriosa</i>	0	0	0	0	0	0	1	17	21	17	2	0

^a Two miles north of Portal, Arizona, August 17, 1970.

Time intervals as in table 1. Samples taken under overcast sky after night of rain; flowers wet until approximately 7 AM; cool, variable breeze; air temperature at 80 minutes before sunrise, 13°C., 20 minutes after sunrise, 14°C., at 2 hours after sunrise 21°C.

bees fly more rapidly, spend only one or two seconds at each flower, and only visit a few flowers on each plant. However, following a rainstorm, when the flowers are wet, *Protoxaea* spend much more time in individual flowers, vibrating them far more than is usually required to release the pollen. Apparently some of the vibration results in the removal of water. In an extreme case a female spent 29 seconds in this activity.

Females returning to their burrows with loads of pollen enter quickly, ignoring the presence of an observer. However, on returning from the midday nectar flight, they commonly strike the observer about the face and head and enter the burrow less directly. Aggressive behavior by females at the nest site has been reported for *Oxaea* by Truxal (1962) and *Anthophora* by Thorp (1969).

Analysis of data from nest sites and flowers suggests that 19°C. approximates the threshold air temperature for female flight, even after sunrise. This temperature is usually exceeded before the bees leave their burrows suggesting that light intensity may be an overriding factor when air temperatures appear to be adequate for flight. Except for the few instances referred to at the Douglas site and the area 2 miles north of Portal (table 1), *Protoxaea* females were rarely seen in flight more than a few minutes before sunrise. Also, although on most hosts pollen collecting is completed within two hours after sunrise, when early flowering pollen sources are lacking or inadequate, females may turn to other plants with fine pollen grains, such as *Kallstroemia grandiflora*. This was the case at the sites 2 miles east of Douglas in the 1970 and 1971 seasons and 2 miles north of Rodeo in the 1971 season. In these two areas preferred hosts were scarce and *Protoxaea* females met their pollen requirements in part from *Kallstroemia*, which did not present its pollen and nectar until an hour or more after sunrise (table 3). This required an extension of pollen collecting activity beyond mid-morning and on overcast days even later. Also, it introduced competition from *Exomalopsis solani* Cockerell, *Svastra s. sabinensis* (Cockerell), and *Diadasia ochracea* (Cockerell).

MALE AGGREGATIONS

Male territorial behavior is generally at a peak near mid-morning and begins to taper off in the early afternoon. The tapering-off period follows a single, short, midday female nectar flight that terminates the above-ground activity of females for the day. At that time, the previously antagonistic males start to gather in large numbers on selected individual plants where they spend the night in a cluster. The initial selection of a cluster site was not observed by us. Each of the sites we encountered gave the appearance of being well established and were regularly returned to each

TABLE 3
COLLECTIONS OF *Protoxaea gloriosa* AND POLLEN-GATHERING COMPETITORS FROM SITE DOMINATED BY
Kallstroemia grandiflora INTERMIXED WITH A SCATTERING OF ALTERNATE HOST PLANTS^a

	Before Sunrise						After Sunrise							
	40 min.	20 min.	0 (sun)	20 min.	40 min.	60 min.	80 min.	100 min.	120 min.	140 min.	160 min.	180 min.	200 min.	220 min.
<i>Solanum eleagnifolium</i>	0	1	2	1	0	1	0	0	0	0	0	0	0	0
<i>Anthophora montana</i>	0	0	1	2	1	0	1	0	0	0	0	0	0	0
<i>Centris atripes</i>	0	0	1	2	2	1	0	0	0	0	0	0	0	0
<i>Protoxaea gloriosa</i>	0	0	1	2	2	1	0	0	0	0	0	0	0	0
<i>Cassia bauhinioides</i>	0	0	0	1	2	2	0	0	0	0	0	0	0	0
<i>Protoxaea gloriosa</i>	0	0	0	1	2	2	0	0	0	0	0	0	0	0
<i>Calliandra schottii</i>	0	0	0	3	5	19	16	14	12	7	4	4	1	0
<i>Protoxaea gloriosa</i>	0	0	0	0	0	0	1	2	2	1	0	0	0	0
<i>Exomalopsis solani</i>	0	0	0	0	0	0	1	2	2	1	0	0	0	0
<i>Kallstroemia grandiflora</i>	0	0	0	0	0	0	1	2	5	9	19	11	1	1
<i>Protoxaea gloriosa</i>	0	0	0	0	0	0	1	1	3	1	0	1	0	0
<i>Suastra sabinensis</i>	0	0	0	0	0	0	0	0	1	2	1	0	0	0
<i>Diadastia ochracea</i>	0	0	0	0	0	0	0	0	1	2	1	0	0	0

^a Two miles north of Rodeo, New Mexico, August 17, 1971.

Time intervals as in table 1. The sample was taken on a clear, bright day with air temperatures during the first time interval before sunrise varying from 19°C. to 20°C., and during the last time interval after sunrise from 27°C. to 29°C.

afternoon. These involved such diverse situations as the upright stem of the weedy composite *Heterotheca subaxilaris* (Lamarck) Britton and Rusby (Evans and Linsley, 1960), the open empty valves of the dried dehiscent pericarps of *Datura quercifolia* (Cazier and Linsley, 1963), and the branches of the woody shrub *Condalia spathulata* Gray (see below).

On August 14, 1965, at approximately 3 PM, M. E. Irwin discovered a large aggregation of males gathering on a shrub of *Condalia spathulata*, 2 miles east of Portal, Arizona. The sun was above the horizon but a storm was rapidly approaching the area, preceded by a cool breeze; clustering was already well under way. The site was under heavy cloud cover from 4 PM and light rain fell between 4 and 5 PM. When the plant was examined about 6 PM, four clusters of males were found, all on the east-facing side. The largest group contained 1107 males and was attached near the end of a heavily twigged and leafed branch about 6½ feet above ground level. A second group of almost the same size, and at about the same height, was clustered around an abandoned nest of a verdin [*Auriparus flaviceps* (Sundevall)] which was about 3 inches in diameter by 3½ inches in length. Eight hundred fifty-seven males were recovered from this group but a considerable number escaped. Two smaller clusters of 48 individuals each, one near ground level, the other 4½ feet above the surface brought the number of males recovered from this one shrub to 2160.

In order to count and mark the bees, net bags were placed over the clusters on branches but the bird's nest aggregation had to be cut from the tree and dropped into a net bag. During the process, a very strong odor was noticeable and when the bees were massed in the bottom of the bag it was evident that they were giving off considerable heat. This prompted an investigation of temperature ranges in the male aggregations by means of a tele-thermometer (length of probe: 4.5 in.).

The first set of readings was taken on the following morning using the 857 male bird's nest aggregation in the net bag. The probe was inserted into the cluster at about 6 AM, and between 6:26 and 7:30 AM 22 readings were made. During this interval, the air temperature ranged over a 4.4°C. interval, from 19.8°C. to 24.2°C., whereas that in the cluster varied only 1.3°C., being maintained at levels between 22.8°C. and 24.1°C.

A more extensive set of readings was taken during the night of August 20 to 21. On this occasion the males began to aggregate at 2:15 PM in hot, bright sunlight (air temperature 38°C. in the shade, 42°C. in the sun!). The bees were "nervous" until the air temperature dropped to 28°C., but consistent readings could not be obtained until 8:45 PM. Readings were then taken at five-minute intervals until 8:45 AM when the last males left the site. Between 8:45 PM and 5:40 AM (sunnise, with sun on cluster), the

TABLE 4
TIME-TEMPERATURE RELATIONS DURING MORNING BREAK-UP OF
AN AGGREGATION OF 549 MALES OF *Protophila gloriosa*^a

Time Intervals	Male Departures	Temperatures in Cluster	Air Temperatures in Shade
5:40-6:33	0	20.5-24.5°C.	18.5-24.0°C.
6:34-7:00	13	24.5-28.0°C.	24.0-25.5°C.
7:01-7:30	176	28.0-30.8°C.	25.5-26.0°C.
7:31-8:00	175	30.8-32.5°C.	26.0-27.8°C.
8:01-8:30	156	30.0-32.5°C.	27.8-29.5°C.
8:31-8:46	29	32.0-32.5°C.	28.8-29.5°C.

^a Two miles east of Portal, Arizona, August 21, 1965. (Sunrise: 5:40 AM.)

air temperature ranged over 5.5°C., from 23.5°C. to 18°C. and that in the cluster on the whole, over 6.0°C. from 20.5°C. to 26.5°C. However, during this period the temperatures in the cluster fluctuated, particularly when disturbed, low points being followed by abrupt rises. For example, at 10:15 PM the cluster temperature was 26.6°C. but at 10:30 PM had risen to 32.2°C. then dropped back to 29.9°C. by 10:40 PM and 28.8°C. by 10:45 PM, 27.7°C. at 10:50 PM, 27.2°C. at 10:55 PM, 25.5°C. at 11:04 PM and continued downward to a low of 22.7°C. at 11:45 PM (air temperature, 20.8°C.). This low point was immediately followed by a rise to 24.5°C. However, low readings at 2 AM (20.5°C.) and 4 AM (19.9°C.) were not followed by heating of the cluster. From 12:30 AM until 5:45 AM there was no visible movement among the bees and the temperatures in the cluster were only 1 or 2 degrees below those of the outside air. Earlier, when heating up, the clusters often vibrated, with the bees on the outside of the mass pumping the abdomen and vibrating the wings slightly. At other times only a few of the outside bees seemed to be involved and these limited their activity to pumping the abdomen.

In the morning, when the cluster was in direct sunlight with the air temperature rising rapidly, the temperature in the aggregation rose from 20.5°C. at 5:40 AM to 24.5°C. at 6:34 AM when the first male left. Thereafter, as each bee left it came to the outside of the cluster, "cleaned" itself with the mouthparts and legs, and defecated an amber liquid which was squirted away from the mass to a distance of 10 to 14 inches, then oriented and flew away. The times of departure and the temperatures in the cluster during five intervals between 6:34 and 8:46 AM are listed in table 4.

The morning orientation flight is made first in front of the limb on which the cluster is situated and then is followed by several large circles around

the entire bush. When the males return in the afternoon the procedure is reversed, with large flight circles followed by smaller ones in front of the specific limb of the plant used by the aggregation.

On the morning of August 20, 1965 at 7:47 AM, one of the males established his territory about 15 feet north of the cluster and proceeded to attack the other males as they left the aggregation until 8:46 AM when all were gone. There were 191 bees still in the cluster when this behavior began.

The bee clusters have an odor which may be due, at least in part, to the morning excrement that stains the leaves and branches with which it comes in contact. The Verdin nest that contained one aggregation was stained yellow. Two species of *Polistes* are evidently attracted by this excrement and appeared to feed on it. These wasps were seen in late evening coming to the limbs with the gathering bees and sometimes walked over them without causing excitement.

For comparative purposes we recorded temperatures of escaped honey bees (*Apis mellifera* Linnaeus) nesting in an old sycamore stump. During the night, outside air temperatures ranged from 20.5°C. to 25.5°C., those in the massed bees from 32°C. to 35°C. These readings for the honey bees are within the range of hive temperatures reported by Dunham (1929), Simpson (1961), and others and were comparable with those of disturbed male *Protopxaea* aggregations. Among the honey bees, some individuals, at least on the outside layers, were moving about and pumping their abdomens in and out most of the time [for references to variation in behavior of honey bees in hives see, for example, Allen (1959), Heran (1952)]. Among the male *Protopxaea* such movements were usually evident only when the bees first clustered and when they began to "wake up" in the morning. During the latter part of the night, they were quiescent and no heat was generated. The lag in temperatures between the inside of the cluster and the outside air observed during this period may have reflected insulation of the probe by the bodies of the bees.

Temperatures taken in nests of *Bombus sonorus* in rodent burrows varied during the night from 22.°C. to 27.°C. During this period, the air temperatures outside of the nests ranged from 14.°C. to 24.°C. This range is comparable with nest temperatures recorded for European bumblebees by Linhard (1912), Himmer (1933), Nielson (1938), and Cumber (1949).

In an attempt to determine how far the males might fly to reach the aggregation site, the dwindling experimental cluster was collected at 6 AM when it contained 344 males. These were marked in various colors on the mesonotum with a small spot of airplane "dope" and released at five different points between 9:30 and 9:46 AM as follows:

Gray: 75 ♂—1 mi. W site behind a ridge (site not visible)
Olive: 65 ♂—2 mi. W site behind a ridge (site not visible)
Green: 74 ♂—1 mi. E site (site visible)
Brown: 65 ♂—3 mi. E site (vicinity of site visible)
Blue: 65 ♂—5 mi. E site (vicinity of site visible)

At each release point the males made one or two circling orientation flights and then flew off.

The following morning the cluster was again collected from the same branch and was found to contain 159 unmarked males and 22 marked ones. Of the marked bees, five had returned from the release point 1 mile west (6.6% of releases), four from 3 miles east (6.1%), and two from 5 miles east (3% of the releases). (This low rate of return was possibly the result of the orientation flights at time of release which may have "masked" previous landmarks and caused the males to return to the release areas rather than the former aggregation site). The 159 unmarked males were marked with silver and released across the San Simon Valley at a point 10 miles from which the site was visible. The next morning one of these was back on the aggregation branch.

We have been unable to find comparable flight records for males of other solitary bees. The fact that females fly long distances has been recorded several times (e.g. Cheesman, 1929; Rau, 1929, 1931; Jansen, 1971). Cheesman, speculating that the Galápagos carpenter bee might fly between islands in the archipelago, reported twice seeing a female flying out at sea some distance from land, in one case coming from an island 8 miles distant. Rau took males and females of *Xylocopa virginica* (Linnaeus) and *Anthophora abrupta* Say in covered cages varying distances away from the nest site and for the female carpenter bees had a high percentage return (65%) a lesser return for females of the mining bee. No males of either species returned. For the *Xylocopa*, 84 percent of the females returned when released within 3 miles of the nest site; 15 of 54 which were released at distances of 5.75 to 7.75 miles. In the cases recorded by Cheesman, the boat apparently provided a focal point for the bees, although they kept on going after passing over it. The Rau experiments were carried out along the Missouri River and railroad tracks which apparently were familiar landmarks to the older bees. Jansen (1971) calculated that female euglossine bees travel as much as 24.4 km. when foraging and are able to find their way back to the nest when removed as far as 23 km.

SIGNIFICANCE OF MALE AGGREGATIONS

Various kinds of "sleeping" aggregations comprising single species,

mixed species, one or both sexes, groups of individuals separate but in close proximity or in dense clusters, have been described (for references see Linsley, 1958; Evans and Linsley, 1960; and Linsley, 1962). Several attempts have also been made to explain these phenomena in evolutionary terms, none of which has been widely accepted. For example, Grassé (1942) considered gregarious sleeping as a possible stage in the evolution of social habits. This might be so but it does not explain the selective value of the habit in presocial evolutionary stages. Evans and Linsley (1960) stated that the most obvious explanation appears to be that the aggregations serve a protective function. However, they emphasized that most aggregations begin to form in daylight hours when diurnal predators are still active. They cited the following observations: "On July 24, 1959, in a patch of milkweed (*Asclepias subverticillata*) near Rodeo, New Mexico, males of *Nomia tetrazonata* Cockerell were beginning to aggregate at 4:15 PM in dense groups estimated at from 10 or 12 to 35 or 40 individuals. The aggregations were noisy and were being preyed upon by a robber fly (*Mallophora bromleyi* Curran), three of which were found in the vicinity with male *Nomia* as prey. In the same area on August 3, 1959, some 25 to 30 males of *Protoxaea gloriosa* were gathering noisily in a ball about half way up a 5 foot plant of *Heterotheca subaxillaris* at 3:50 PM. The sky was clear, the sun bright and warm, and again asilids were active in the vicinity. An example of *Blepharepium secabilis* (Walker) was taken with *Protoxaea* as prey, another turned up in the net when an attempt was made to sweep up the aggregation for counting and identification."

However, in spite of this evidence of vulnerability to predation during assembly, the selective value of dense sleeping aggregations must be significant as the habit appears to have arisen independently a number of times among bees and other aculeate Hymenoptera. Among bees, the genera involved are mostly regarded as relatively low in the phylogenetic scale (see classification of Michener, 1965) although not necessarily unspecialized (e.g. *Leioproctus*, *Paracolletes*, *Stenotritus*, *Protoxaea*, *Nomia*, etc.).¹ The discovery that at least some of the species in which males gather in clusters are able to produce heat² adds weight to the suggestion that such

¹ We have not observed gregarious sleeping among males of the large colletid competitors of *Protoxaea* in southwestern United States, e.g., *Caupolicana* and *Ptiloglossa*. Linsley (1962) reported a few instances of *C. yarrowi* males sleeping individually on stems of *Melilotus albus*, attached by the mandibles. In view of the large numbers of *Ptiloglossa* in the areas under study, the absence of male aggregations appears to be significant.

² Rayment (1935) speaking of clusters of males of *Stenotritus pubescens* (Smith), commented that "Certainly, there is not the ordered arrangement of the worker-bees of the

aggregations are defensive in nature. Thus, when quiescent clusters of male *Protoxaea* are disturbed the temperature will rise to 32°C. or more in less than a minute, a reaction which might permit the bees to escape predators by flight.

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